Chapter 14

Broca's area in language, action, and music

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Summary

The work of Paul Broca has been of pivotal importance in the localization of some higher cognitive brain functions. He first reported that lesions to the caudal part of the inferior frontal gyrus were associated to expressive deficits. Although most of his claims are still true nowadays, the emergence of novel techniques as well as the use of comparative analyses, prompt modern research for a revision of the role played by Broca's area. Here we review current research showing that the inferior frontal gyrus and the ventral premotor cortex are also activated for tasks other than language production. Specifically, a growing number of studies report the involvement of these two regions in language comprehension, action execution and observation, music execution, and listening. Recently, the critical involvement of the same areas in representing abstract hierarchical structures has been further demonstrated. Language, action, and music share a common syntax-like structure. We propose that these areas are tuned to detect and represent complex hierarchical dependencies, regardless of modality and use. We speculate that this capacity evolved from motor and premotor functions associated with action execution and understanding, such as those characterizing the mirror-neuron system.

The role of Broca's area in language

The earliest attempts to localize the seat of language in the human brain were made by researchers in the field of phrenology, who located this faculty in the frontal lobes, bilaterally. This idea found support in a series of clinical cases showing that lesions located in the anterior lobes of the brain consistently impaired language functions without destroying general intelligence. Marc Dax, during the first years of the 19th century, concluded that the loss of language was more frequently associated with damages to the left half of the brain (McManus, 2002). The French neurologist Paul Broca was the first in establishing that the posterior part of the left inferior frontal gyrus (IFG) was of critical importance for language production. Broca's famous case, named 'Leborgne', suffered from left frontal damage extending from the inferior part of the third frontal circumvolution to the insula and the striatum (Dronkers *et al.*, 2007). Broca's aphasia was thus described as a

syndrome characterized by effortful speech production, impairment in melodic line and articulation, semantic and phonemic paraphasias, production of telegraphic sentences, and reduced and abnormal grammatical form (Alexander *et al.*, 1990; Caplan *et al.*, 1996).

Modern textbooks consider Broca's 1861 paper as a landmark point for language localisation research, as well as for the localisationist approach in general. However, many of his contemporaries were reluctant to accept his data as a conclusive proof of his own claims. First, Broca had to overcome the resistance of Bouillaud, whose proposal about 'organic duality and functional unity' opposed a preeminence of the left frontal lobe in speech production. Moreover, his localisationist ideas were challenged by Jackson's dynamic model of language (Berker *et al.*, 1986). In more recent times, and despite the emergence of modern techniques, a final agreement regarding the precise localization of several aspects of language competence remains to be determined.

The neurosurgeon Wilder Penfield was the first to experimentally demonstrate the involvement of Broca's region in speech production by electrically stimulating the frontal lobe in awake patients undergoing brain surgery. He reported that the stimulation of Broca's area evoked the arrest of ongoing speech, although with some individual variability (Penfield & Roberts, 1959). However, in subsequent decades, a series of experiments demonstrated that both Broca's and Wernicke's (*i.e.*, the temporal area classically considered the site for speech perception) areas are implicated in both the comprehension and production aspects of language (Ojemann *et al.*, 1989; Schaffler *et al.*, 1993). The electrical stimulation of Broca's area produced marked interference with language output functions as well as language comprehension deficits (Schaffler *et al.*, 1993). These receptive deficits were predominantly in response to complex auditory verbal instructions.

Recently, a more detailed description of frontal aphasic patients have included a varying degree of speech comprehension deficits. These deficits became more evident when the patients were tested with verbal material requiring syntactical understanding (Alexander *et al.*, 1990; Caplan *et al.*, 1996). Thus, the functional segregation between Broca's and Wernicke's areas could rather be associated with their different encoding of syntax. In fact, it has been found that that Broca's area is preferentially engaged during language comprehension of syntactically complex and/or ambiguous material (Fiebach *et al.*, 2004).

Current models of language brain processing posit an important role of network dynamics. In fact, several temporal, parietal, and frontal areas interact in order to deliver the many features of language ability. Cortico-cortical evoked potentials demonstrate a functional bidirectional connectivity between anterior and posterior language areas (Matsumoto *et al.*, 2004). The degree of connectivity among language brain areas was shown to be affected by task characteristics and has been found altered in patients with primary progressive aphasia (Londei *et al.*, 2007; 2009; Sonty *et al.*, 2007). The functional connection between anterior and posterior language areas has been classically considered to be mediated by the arcuate fasciculus. Recently the anatomic connectivity pattern between Broca's and Wernicke's areas as well as the inferior parietal lobule (Geschwind's territory) have been assessed using diffusion tensor imaging (Catani *et al.*, 2005). According to this study, these three territories form a trianglelike functional structure mediated by the long segment fibers (Wernicke's to Broca's), posterior segment fibers (Wernicke's to Geschwind's), and anterior segment fibers (Geschwind's to Broca's) (Catani *et al.*, 2005).

The arcuate fasciculus has also been found to be significantly larger in the left hemisphere, thus supporting its critical role for language (Glasser & Rilling, 2008). Interestingly enough, a recent comparative study measured the macaque's, chimpanzee's, and human's arcuate

fasciculi, describing a huge qualitative change between the macaque and the chimpanzee. More-over, the dorsal branches passing through the inferior parietal lobule were almost absent in the macaque and more similar between humans and the chimpanzees (Rilling *et al.*, 2008). The discovery of dissociable functions for Broca's and Wernicke's areas was a landmark in the history of neurology, prompting an antero-posterior distinction between language-related brain areas. However, several modern lines of research suggest a more integrated and dynamic view of language brain functioning. On the basis of these data, one can conclude that the role of Broca's area is not limited to speech production, but extends to speech comprehension as well. These models suggest that the anatomic connection and concerted activity among posterior and anterior language areas could be a critical feature for the deployment of the language ability (Pulvermuller, 2005; Warren *et al.*, 2005; Skipper *et al.*, 2006).

Evolutionary origin of Broca's area

Neuroanatomic studies of Broca's area, and in particular of its pars opercularis (BA44), show that some cytoarchitectonical properties are shared with premotor cortex (BA6). Indeed, the granular cells layer (the IV cortical layer), which is clearly absent in BA 6, is slightly present in BA 44. The frontal cortex becomes in fact clearly granular only in area 45, the pars trian-gularis of the inferior frontal gyrus. From a cytoarchitectonic point of view (Petrides & Pandya, 1997), the monkey's frontal area, which closely resembles the human Broca's region, is the agranular/dysgranular premotor area (area F5) (Matelli *et al.*, 1985). More recently, attention has been focused on the parcelization of monkey area F5 (Petrides *et al.*, 2005), showing that the caudal bank and the fundus of the arcuate sulcus differ one from the other as far as cytoarch-itectonics is concerned. While the bank is mainly agranular, the fundus is dysgranular. More-over, this last sector of area F5 remains clearly distinct from the contiguous anterior bank, a region that both studies consider as pertaining to prefrontal cortex (Fig. 1).

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Microstimulation and single-neuron studies showed that hand and mouth movements are rep-resented in area F5 (Hepp-Reymond *et al.*, 1994; Rizzolatti *et al.*, 1988). Most of the hand neurones discharge in association with goal-directed actions such as grasping, manipulating, tearing, and holding, while they do not discharge during similar movements when made with other purposes (*e.g.*, scratching or pushing away). Furthermore, many F5 neurones become active during movements that have an identical goal regardless of the effectors used for attaining it, suggesting that these neurones are capable of generalizing the goal, independent of the acting effector.

F5 neurones can be subdivided into several classes: 'grasping', 'holding', ' tearing', and ' manipulating' neurones. Grasping neurones form the most represented class in area F5. Many of these are selective for a particular type of prehension such as precision grip or whole-hand prehension. In addition to their motor discharge, however, several F5 neurones also discharge to the presentation of visual stimuli (visuomotor neurones). Two radically different categories of visuomotor neurones are present in area F5: canonical and mirror neurones. Canonical neu-rones discharge when the monkey observes graspable objects (Rizzolatti *et al.*, 1988; Murata *et al.*, 1997), whereas mirror neurones discharge when the monkey observes another individual making an action in front of it (Gallese *et al.*, 1996; Umiltà *et al.*, 2001). When comparing visual and motor properties of canonical neurones in F5, it becomes clear that there is a strict congruence between the two types of responses. Neurones becoming active when the monkey

observes small-size objects, also discharge during precision grip. On the contrary, neurones selectively active when the monkey looks at a large object discharge also during actions directed towards large objects (*e.g.*, whole-hand prehension) (Murata *et al.*, 1997). The most likely interpretation for the visual discharge of these visuomotor neurones is that, at least in adult individuals, there is a close link between the most common 3D stimuli and the actions necessary to interact with them. Thus, every time a graspable object is visually presented, the related F5 neurones are activated and the action is 'automatically' evoked. Under certain circumstances, it guides the execution of the movement, whereas under others, it remains an unexecuted representation of it.

Mirror neurones become active when the monkey acts on an object and when it observes another monkey or the experimenter making a similar goal-directed action, therefore being identical to canonical neurones in terms of motor properties. However, they radically differ from them as far as visual properties are concerned. Typically, mirror neurones show congruence between the observed and executed action. This congruence can be extremely strict, that is, the effective motor action (*e.g.*, precision grip) coincides with the action that, when seen, triggers the neurones (*e.g.*, precision grip). For other neurones the congruence is broader. For them the motor requirements (*e.g.*, precision grip) are usually stricter than the visual ones (any type of hand grasping) (Rizzolatti *et al.*, 1988).

In considering all the functional properties of neurones in this region, it appears that in area F5 there is a storage, a 'vocabulary', of motor actions related to hand use. The 'words' of the vocabulary are represented by populations of neurones. Each indicates a particular motor action or an aspect of it. Some indicate a complete action in general terms (*e.g.*, take, hold, and tear). Others specify how objects must be grasped, held, or torn (*e.g.*, precision grip, finger prehension, and whole-hand prehension). Finally, some subdivide the action into smaller segments (*e.g.*, fingers flexion or extension). It seems plausible that the visual response of both canonical and mirror neurones target the same motor vocabulary, the words of which constitute the monkey motor repertoire. What is different is the way by which 'motor words' are selected: in the case of canonical neurones they are selected by object observation; in the case of mirror neurones by the sight of an action. This purported motor 'vocabulary' is therefore formed by objects and actions. Both are represented in terms of doable actions in the environment (Rizzolatti *et al.*, 2001).

Broca's area in action

A growing body of neuroimaging evidence indicates that Broca's area, in addition to its linguistic functions, appears to be engaged in several cognitive domains. These domains include music, working memory, or calculation (Fadiga *et al.*, 2006). Another important contribution of BA44, in analogy with monkey studies, is found in the motor domain. The activity of Broca's area was found when categorizing man-made objects as compared to natural ones and when subjects were required to represent possible actions upon manipulable objects (Gerlach *et al.*, 2002; Kellenbach *et al.*, 2003). These authors proposed that artifact observation and object manipulability enable a richer motor-based representation. Several other studies also reported a significant activation of BA44 during execution of distal movements such as grasping (Binkofski *et al.*, 1999; Gerardin *et al.*, 2000). Moreover, the activation of BA44 is not restricted to motor execution, but is partially shared with motor imagery (Gerardin *et al.*, 2000; Lotze & Halsband, 2006).

Passive observation of graspable objects, in accordance with the canonical-neuron system in the monkey, was found to elicit motor, premotor, and inferior frontal activities in humans (Grafton *et al.*, 1997). Subjects were scanned during observation of bidimensional colored pictures, observation of 3D objects (real tools attached to a panel), and during silent naming of the presented tools or descriptions of their use. The premotor cortex became active during the simple observation of tools and this activity was further augmented when the subjects named tool use. A PET study indicated that the perception of objects versus perception of nonobjects, irrespective of the task asked of the subject, was associated with left-hemisphere activations of the occipito-temporal junction, the inferior parietal lobule, the SMA-proper, Broca's area, and the dorsal and ventral precentral gyrus (Grezes & Decety, 2002).

Several other experiments studied brain activity while the participants observed actions made by human arms or hands (Fadiga *et al.*, 1995). Activations were present in the ventral pre-motor/inferior frontal cortex with a functional pattern analogous to that of mirror neurones in the monkey (Buccino *et al.*, 2001; Binkofski & Buccino, 2006). Accordingly, it has been demonstrated that during the observation of meaningless gesture there was no Broca's region activation when compared with transitive (goal-directed) gestures (Grezes *et al.*, 1999) and that a meaningful hand-object interaction is more effective in triggering Broca's area activation than is pure movement observation (Johnson-Frey *et al.*, 2003).

Summing up, neurophysiologic (Fadiga *et al.*, 2005) and brain-imaging experiments (Rizzolatti & Craighero, 2004a) prove that both the canonical-neuron and the mirror-neuron systems exist in humans. Unfortunately these sources of information (neuroimaging and electrophysiologic techniques), although very compelling, offer only a correlation between the activity of a given area and the task the subject is performing. The causal determination of the role played by Broca's area in object affordances generation and action representation require other more stringent methodologies.

A lesion to Broca's area typically produces a dramatic expressive language deficit. Neuropsy-chological studies on patients with frontal aphasia have shown deficits in several aspects of the motor domain in line with the role that Broca's area plays in such mechanisms. Supralinguistic impairments were described that also affected such nonverbal abilities as recognizing signs, gestures, and pantomimes (Rizzolatti & Craighero, 2004b; Tranel *et al.*, 2003). Tranel and colleagues demonstrated that left frontal brain-damaged patients have difficulties in under-standing action details when presented with cards depicting various actions (Tranel *et al.* 2003). Furthermore, it has been demonstrated that patients with aphasia show a correlation between action comprehension (through pantomime interpretation) and reading comprehension deficits (Saygin *et al.*, 2004). However, in these studies, the task consisted in asking patients to answer a verbally posed question, so it is therefore possible that these patients may have had troubles in performing the task because of its linguistic nature. Moreover, it is often unclear whether this relationship between aphasia and gesture recognition deficits is due to a Broca's area lesion only or whether it depends on the involvement of other neighboring areas. Indeed, it is known that aphasic patients have a complex pattern of symptoms and are sometimes also affected by apraxia (Goldenberg, 1996). Recently, it has been demonstrated that limb apraxic patients (along with an important production aphasia) had an impairment in gesture comprehension, the severity of which correlated with the extension of lesions in the pars opercularis and in the pars triangularis of the left IFG (Goldenberg, 1996).

In order to avoid the presence of inherent linguistic distortions and the confounding factors played by apraxia, we tested frontal aphasic patients without praxis disturbances by using a novel action-understanding task with no linguistic requirements. Patients were requested to

correctly sequence randomly mixed pictures taken from video clips representing various human actions (*e.g.*, a hand grasping a bottle). Physical events (*e.g.*, a bicycle falling) were used as a control. In order to complete the task one has to understand the general goal of the action first, and then be able to correctly re-order images representing simpler motor acts. We found a specific deficit in pragmatically representing the correct sequence of the individual motor acts forming an action, together with a preserved capability in performing the same task with physical events. In such a way we empirically demonstrated the role of Broca's area in action understanding (Fazio *et al.*, 2009).

Broca's area in music

The discovery of tri-modal (motor, visual, and auditory) mirror neurones in the monkey ventral premotor cortex has encouraged studies of the auditory properties of the human mirror-neuron system (Kohler *et al.*, 2002). This putative mechanism is thought to map the acoustic representation of actions into the motor plans necessary to produce those actions. Action-related sounds were found to activate the inferior frontal gyrus in addition to the superior temporal gyrus (Pizzamiglio *et al.*, 2005). Sounds executed by the hand or the mouth activate premotor areas in a somatotopic manner in humans (Gazzola *et al.*, 2006). Lewis and colleagues (2005) found that tool sounds preferentially activated a cortical mirror-like network. This network directly overlapped with motor-related cortices activated when participants pantomimed tool manipulations. Warren and colleagues (2006) demonstrate that listening to nonverbal vocalizations can automatically engage the preparation of responsive orofacial gestures, an effect that is greater for positive valence and highly arousing emotions. Summing up, sound associated with movement, such as action sounds, tool sounds, or vocalization, activate the same structures necessary for the production of similar sounds. Listening to these sounds enables the study of simple auditory-motor interactions.

Other studies have investigated the brain areas activated in more complex action-related sounds such as music. Musicians are a particular class of experts who master the ability to map sounds onto movements. Experts have already proved to be an interesting model of overlearned perceptuo-motor associations. Dancers and sport players observing and evaluating actions within their field of expertise indeed demonstrated a higher motor awareness (Calvo-Merino *et al.*, 2006; Aglioti *et al.*, 2008). Experts, by definition, are subjects who decide to train a particular skill extensively, just as professional musicians do for hours a week. Musicians, in fact, are revealed to be subjects of great interest in the study of how specific training can enlarge somatosensory representation of digits used in practicing an instrument (Elbert *et al.*, 1995). Similarly, the motor system undergoes important plastic changes with specific practice in musicians (Pascual-Leone *et al.* 1995), and auditory representations were found to be enlarged specifically for musical tones (Pantev *et al.*, 1998). Musicians have also been used to investigate both long-term structural and short-term functional brain plastic changes (Schlaug *et al.*, 1995; Rosenkranz *et al.*, 2007). Sensorimotor plasticity in musicians is the result of repeated co-occurrences of specific actions and the associated sensory effects (Munte *et al.*, 2002).

A growing number of studies have focused on the mechanisms for the integration of audio-motor information (Zatorre *et al.*, 2007). A number of neuroimaging researchers have recently addressed this issue from different perspectives. On the one hand, it has been found that motor and premotor activities could be elicited in experts by passive listening to known melodies. For instance, the activity of motor centers of expert pianists was enhanced while they were listening to piano pieces (Haueisen & Knosche, 2001). Furthermore, several fMRI studies

looked for common activations between perception and production of a musical piece (Bangert & Altenmuller, 2003). These studies confirmed the existence of a complex brain network, including motor, premotor, and supplementary motor areas, the inferior parietal lobule, and the superior temporal gyrus. On the other hand, others studies have focused their attention on the role of training in nonexperts. An EEG study showed increased sensorimotor activity in naïve subjects after a short period of musical training, both during observation of muted piano movements and during passive listening (Bangert *et al.*, 2006). Interestingly, a TMS study further demonstrated that even after 30 minutes of practice, the passive listening of a trained piece increased the facilitation of listeners' primary motor cortex (D'Ausilio *et al.*, 2006). On the same line, it has been shown that, in nonmusicians, premotor activity was specifically increased by passive listening to a trained piece, but not to a different combination of the same notes (Lahav *et al.*, 2007).

Musical imagery research is a particularly interesting domain of study, dealing with the ability of re-enacting musical experience, whether motor, auditory, or both. During these tasks, musicians activate a network of areas similar to that outlined for the passive listening and performance of a musical excerpt (Zatorre & Halpern, 2005; Langheim *et al.*, 2002). Therefore, it is possible to delineate a network of brain areas shared between listening, producing, and imaging musical excerpts. This network includes the STG, the IPL, and motor/premotor regions, and is active in both experienced musicians (Haueisen & Knosche, 2001; Bangert *et al.*, 2006; D'Ausilio *et al.*, 2006), and in naïve subjects after a proper training (Bangert & Altenmuller, 2003; Lahav *et al.*, 2007; D'Ausilio *et al.*, 2006). Such brain circuitry shows close similarities to that found in language studies (Gernsbacher & Kaschak, 2003) and, intriguingly, with the pattern of cortical activity often reported in action execution/observation research (Rizzolatti & Craighero, 2004a). Thus, it is likely that listening to musical excerpts (after proper motor training) activates motor representations required for the actual production of those melodies, with a mirror-like mechanism. In fact, musical excerpts might be considered as actions whose motor representation are preferentially triggered by auditory stimuli (Lahav *et al.*, 2007; D'Ausilio 2007)

Another interesting parallel between language and music is the similar intrinsic complexity of musical and language structures. In fact, there are more homologies between these two domains than might be expected on the basis of dominant theories of musical and linguistic cognition–from sensory mechanisms that encode sound structure to abstract processes involved in integrating words or musical tones into syntactic structures (Patel, 2003). In an elegant study, Maess and colleagues (2001) located the seat of musical syntax in the bilateral inferior frontal gyrus. Indeed, on several occasions, the predictability of harmonics and the rules underlying music organization have been compared to language syntax (Patel, 2003). By inserting unexpected harmonics Maess and coworkers (2001) created a sort of musical 'syntactic' violation. Using magnetoencephalography (MEG) they studied the neuronal counterpart of hearing harmonic incongruity and they found an early right anterior negativity (ERAN) usually associated with harmonic violations (Koelsch *et al.*, 2000). A similar fMRI study revealed that the human brain network involved in processing musical information has strict similarities with that for processing language. Broca's and Wernicke's areas, the superior temporal sulcus, Heschl's gyrus, plana polaris and temporalis, as well as the anterior superior insular cortices were all found activated while subjects listened to unexpected musical chords (Koelsch *et al.*, 2002). Tillmann and colleagues (2003) investigated the neural correlates of processing harmonically related and unrelated musical sounds in a classical priming paradigm. These behavioral studies showed that the processing of musical targets is faster and more accurate when it is harmonically

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related to the preceding stimuli. Moreover, the blood oxygen level-dependent (BOLD) signal measured by fMRI in the IFG was stronger for unrelated than for related targets. This result has been interpreted as a proof that the inferior frontal cortex is involved in the processing of syntactic relations and in favor of its role in processing and integrating sequential information over time.

Summing up, several EEG/MEG studies have found the emergence of an early right anterior negativity (ERAN around 200 ms) when subjects were presented with structurally irregular chords (Maess *et al.*, 2001; Koelsch *et al.*, 2000). More interestingly, the ERAN is very similar to another deviance-related negativitiy, such as the early left anterior negativity (ELAN), which reflects the processing of syntactic structures in language (Friederici, 2002). The generator of the ERAN was localized in BA44 (Maess *et al.*, 2001) in accordance with other fMRI studies using similar paradigms or using paradigms studying the processing of harmonic, melodic, or rhythmic structures (Koelsch, 2006).

Broca's area and supramodal representations

The overall picture about Broca's area in cognition suggests a pivotal role in critical domains such as language, action, and music. Broca's area involvement in language production has a long history, solidly built upon 150 years of lesion studies and corroborated by modern neuroimaging and neurophysiologic techniques (Gernsbacher & Kaschak, 2003). Recently, though, its role has been extended to receptive functions as well, in the context of integrated brain network models (Pulvermuller, 2005). Although the functional connection and relation between productive and receptive mechanisms is an old scientific question (James, 1890), only in recent years has a renewed interest fostered substantial scientific advancements. This new interest is partly due to neurophysiologic studies on the monkey (Rizzolatti & Craighero, 2004a). These studies, describing neuronal mechanisms for matching executed and observed actions, motivated numerous neuroimaging and neurophysiological studies in search for similar mechanisms in humans. Broca's area was found to be at the center of a brain network for the encoding of action goals, either observed or executed (Rizzolatti & Craighero, 2004a). Moreover, action representation in Broca's area was also demonstrated to be triggered by its acoustical counterpart, both in the monkey and in humans (Kohler *et al.*, 2002; Gazzola *et al.*, 2006; Lahav *et al.*, 2007), and finally Broca's area was found implicated in the encoding of musical syntax in much the way it encodes language structures (Koelsch, 2006).

Lesion studies have demonstrated that lesions situated in the pars opercularis and in the pars triangularis of the left IFG lead to an impairment in gesture comprehension (Pazzaglia *et al.*, 2008). These results are also in line with those reported by Tranel and colleagues (2003), demonstrating that left frontal brain-damaged patients have difficulties in understanding action details when presented with cards depicting various actions. The basic idea that Broca's area is involved in action representation (in broad terms) is also supported by the reported deficit of these patients in specifically representing action verbs (Gainotti *et al.*, 1995). Moreover, we tested patients with a lesion centered in Broca's area with an action-sequencing task, and our results suggest the intriguing possibility that Broca's area could represent action's syntactic rules rather than the basic motor program to execute them (Fazio *et al.*, 2009).

Actions are denoted by a relevant behavioural goal that, in order to be achieved, requires the composition of simpler motor acts. Single motor acts do not necessarily posses a goal that motivates their execution. On the other hand, the same motor act might be part of very different actions, associated with different goals. Typically a goal-directed action might be 'to drink' or

'to displace', and reaching for a glass might be associated with both of these goals without evident differences in kinematics. At the same time, the 'drinking' action-prototype might be composed by several acts such as 'reach' for the glass, 'bring' it to mouth, and 'swallow', but can also be satisfied by using a completely different set of acts such as the case of drinking from a public fountain. Actions and motor acts are also composed of simpler units representing the spatiotemporal sequence of muscle activations (Grafton & Hamilton, 2007). These action hierarchies resemble the complex structures shown in other domains, such as music and language and, more interestingly, the experimental manipulation of these complex structures is associated with the activation of premotor and Broca's areas, regardless of the domain of study (*i.e.*, music or language).

Hence we propose that Broca's area might be a center of a brain network encoding hierarchical structures regardless of their use in action, language, or music. This hypothesis is also in agreement with recent studies demonstrating that patients with lesions of Broca's area are also impaired in learning the hierarchical/syntactic structure, but not the temporal one, of sequential tasks (Dominey *et al.*, 2003; Sirigu *et al.*, 1998). The shared feature of music, language, and action may therefore be their use of hierarchical/syntactical structures, and these results support the idea of a supramodal role for BA44. A recent study using event-related fMRI succeeded in disentangling hierarchical processes from temporally nested elements (Koechlin & Jubault, 2006). These authors reported that Broca's area and its right homologue control selection and nesting of action segments, integrated in hierarchical behavioural plans, regardless of their temporal structure. In fact, when comparing the processing of hierarchical dependencies to adjacent dependencies, subjects show significantly higher activations in Broca's area and in the adjacent ventral premotor cortex (Bahlmann *et al.*, 2008). These results indicate that Broca's area is part of a neural circuit that may be responsible for the processing of hierarchical structures in an artificial grammar.

Although the proposal that Broca's area could encode a supramodal syntax might seem intriguing, several questions yet remain to be addressed. On a theoretical level a definition is needed as to how, and to what extent, syntactic structures in these domains (action, language, and music) share similar mechanisms and how they interact. Anatomically speaking, we need more data on the degree of overlap (and/or segregation) between activities associated with syntax encoding in all these different domains. Finally, the degree of innateness and plasticity of such a syntactic representation remains somewhat obscure. If on the one hand we might think that syntactic complexity grows with experience, on the other hand, it seems that a basic sensitivity to a set of grammatical rules is already present at birth, regardless of linguistic experience and exposure. Such a claim is supported by a recent study on newborns showing a preference for sequence of stimuli with a structural regularity (ABB as opposed to ABC), and that processing of these redundant sequences elicits activity in the left inferior frontal gyrus (Gervain *et al.*, 2008). One possible, and reconciling, interpretation is that the organization of sensory and motor events in terms of hierarchical structures might be a necessary step to allow comprehension and encoding of experience, but that, at the same time, the brain is ready for syntax at birth because of its innate capability to deal with (and statistically appreciate) regularities of stimuli.

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*Fig. 1. Human Broca's area and its monkey homologue. (**A**) The anatomic location of monkey area F5, which has been considered the homologue of the human Broca's area. (**B**) Graphic representation of human brain areas which functionally and anatomically resemble monkey area F5. These areas include the ventral premotor cortex (vPM), and Brodmann's area 44 and 45.*